Active Ignoring in Early Visual Cortex

Helen E. Payne and Harriet A. Allen

Abstract

■ Selective attention is critical for controlling the input to mental processes. Attentional mechanisms act not only to select relevant stimuli but also to exclude irrelevant stimuli. There is evidence that we can *actively* ignore irrelevant information. We measured neural activity relating to successfully ignoring distracters (using preview search) and found increases in both the precuneus and primary visual cortex during preparation to ignore distracters. We also found reductions in activity in fronto-parietal regions while previewing distracters and a reduction in activity in early visual cortex during search when a subset of items was successfully excluded from search, both associated with precuneus activity. These results are consistent with the proposal that actively excluding distractions has two components: an initial stage where distracters are encoded, and a subsequent stage where further processing of these items is inhibited. Our findings suggest that it is the precuneus that controls this process and can modulate activity in visual cortex as early as V1. ■

INTRODUCTION

Efficient mental processing requires that we select from the world those stimuli that are behaviorally relevant to our current goals and to ignore those objects that are irrelevant. Attentional selection can enhance the neural processing of attended stimuli, manifested as improvements in reaction time, accuracy, and target detection/discriminability of cued items (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Yeshurun & Carrasco, 1999; Posner, Snyder, & Davidson, 1980). It can also suppress processing of signals evoked by irrelevant stimuli and locations (Sylvester, Jack, Corbetta, & Shulman, 2008; Ruff & Driver, 2006; Serences, Yantis, Culberson, & Awh, 2004). Furthermore, fMRI studies reveal not only a stimulus evoked response to an attended target but also increases in activation in the portions of visual cortex that represent the anticipated location of the stimulus, that is, preparatory activity (e.g., Macaluso, Eimer, Frith, & Driver, 2003; Hopfinger, Buonocore, & Mangun, 2000; Ress, Backus, & Heeger, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). This preparatory activity is thought to bias the visual areas to favor the processing of the subsequent expected target. In the present study, we are interested in the complementary effect, that of preparation to ignore.

Excluding unhelpful or irrelevant stimuli is clearly advantageous. Several behavioral experiments have shown that if the locations of distracters are known, then their detrimental effects on target processing are reduced (Ruff & Driver, 2006; Serences et al., 2004), and this is linked to increased neural activity in visual cortex. Control of attention both to targets and away from distracters is likely to involve a network of fronto-parietal brain regions. Brain regions consistently activated during attentional preparation following a cue include the intraparietal sulcus, frontal eye fields, and the superior parietal lobule (SPL) (Sylvester et al., 2008; Ruff & Driver, 2006; Macaluso et al., 2003; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger et al., 2000; Kastner et al., 1999; Shulman et al., 1999). It is thought that this network of brain regions is important for generating biasing signals that modulate activity in visual cortex (for a review, see Pessoa, Kastner, & Ungerleider, 2003). Given that parts of this network are likely to guide attention toward targets and away from known distracters, it is critical to separate these two processes. The preview search paradigm (Watson & Humphreys, 1997) used here allows the to-be ignored items to be separated in time from the attended items. The preview distracters are presented prior to the addition of the remaining distracters and a target to the display. Search performance improves compared to trials where all items are shown at the same time (a full-set search; Watson & Humphreys, 1997).

Watson and Humphreys (1997) argued that observers actively apply top–down inhibition to the locations of previewed distracters, which they termed *visual marking* (see also Braithwaite & Humphreys, 2003; Olivers & Humphreys, 2003; Watson, 2001). Other accounts have proposed no inhibition of old items and have placed emphasis on attention to the new items. Transient luminance onsets of the new search items may automatically capture attention (Donk & Theeuwes, 2001) or temporal segmentation between the old and new items may guide attention (Jiang, Chun, & Marks, 2002). Behavioral evidence from dual-task studies, on the other hand, (Humphreys, Watson, & Jolicœur, 2002) and probe-dot detection studies (Humphreys,

University of Birmingham, UK

Stalmann, & Olivers, 2004; Olivers & Humphreys, 2002; Watson & Humphreys, 2000) suggests old items in the preview search task are *actively* inhibited. Watson and Humphreys (2000) conducted a standard preview search task but on a minority of trials participants were cued to detect a probe dot. Detection of probes presented at the locations of previewed distracters was impaired (vs. on new distracters), suggesting that information from the locations of the previewed distracters was inhibited. Similarly, comparing cueing to preview search showed that participants were better able to exclude previewed items than noncued items (Allen & Humphreys, 2007a). Effectively, the visual system reduces the contrast of successfully previewed and ignored items (Allen & Humphreys, 2007b).

Preview search, therefore, offers a way to investigate neural mechanisms underlying ignoring known distracters. Recent neuroimaging studies (Dent, Allen, & Humphreys, in press; Allen, Humphreys, & Matthews, 2008; Olivers, Smith, Matthews, & Humphreys, 2005; Pollmann et al., 2003) compared neural activity in response to preview trials to that in response to nonpreview search baseline trials. Trials consisted of two displays. The preview condition first display was a true preview; items remained on the screen when the new items appeared. In the baseline conditions, the items in the first display disappeared and were replaced by distracters in different locations. Thus, the first displays of preview trials and baseline trials were visually identical but the attentional set of the participants was different between the conditions; the first display in baseline trials required only passive viewing, whereas the preview trials would reveal the processes involved with ignoring stimuli. These studies have consistently demonstrated enhanced neural activation in posterior parietal cortex (in particular, the SPL and the precuneus) for preview trials relative to baseline. The SPL/precuneus is proposed to set up a spatial representation of the old previewed distracters so that these items are biased in favor of the subsequently presented new search items. This is supported by computational modeling (Mavritsaki, Allen, & Humphreys, 2009). Mavritsaki et al. (2009) used the spiking Search over Time and Space (sSoTS) model to analyze the preview search fMRI data from Allen et al. (2008) by including inhibition (suppressing old distracters) and excitation (anticipation for target) as regressors and found that the activation in the precuneus reported by Allen et al. could be predicted by the inhibition.

Here we investigate what effect these parietal activations have on visually responsive cortex by presenting stimuli to different retinal locations (i.e., the four visual field quadrants). It is an open question as to what effect previewing distracters has on sensory brain areas. Traditional models of visual attention would predict that unattended stimuli (i.e., uncued) would lead to a decrease in neural activation in brain areas specialized for vision (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Smith, Singh, & Greenlee, 2000). In contrast, when previewing face distracters, Allen et al. (2008) found an increase in activation in face processing areas, even during the initial preview display. This enhanced neural activation in response to the preview trials may reflect an active ignoring process that is distinct from passive viewing (or simply attending elsewhere) of the same stimuli.

If a similar pattern of activation is found in early visual cortex as in category-specific regions, then this might be viewed as a signature for active ignoring. Given that attending to a stimulus at a particular spatial location will enhance striate cortex blood oxygenation level dependent (BOLD) activation (e.g., Gandhi, Heeger, & Boynton, 1999; Martínez et al., 1999; Somers, Dale, Seiffert, & Tootell, 1999), it is important to relate any activation change in early visual areas with successful ignoring rather than simply the intent to ignore. Second, we investigate the functional relationship between activity in precuneus regions and changes in activity in visual cortex. Previously, it has been assumed that if parietal and visual areas both change in activation in preview trials, then one must drive the other. Here, we take this one step further and look for brain regions where activation appears to be part of a functional network and link this to successfully ignoring previewed items.

By using the preview search paradigm, we are able to separate changes in activation related to successful ignoring from changes related to the target. We follow the logic of Dent et al. (in press), Allen et al. (2008), and Pollmann et al. (2003), and include catch trials to measure the pure neural activity associated with previewing informative (i.e., in the preview condition) and uninformative (i.e., in the baseline condition) first displays without any contamination from the neural activity arising from the search displays. This is comparable to experiments (Macaluso et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999) that separate the neural activity associated with the cue (i.e., the preparatory activity) with that associated with the target.

METHODS

Participants

Eighteen paid participants (14 women, 18–35 years old, $M = 24.3$ years) gave written informed consent in accordance with the ethical procedures of the Birmingham University Imaging Centre, Birmingham, UK. All had normal or corrected-to-normal vision.

Stimuli and Apparatus

Experiments were created in Matlab (The Mathworks, Natick, MA) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The distracter stimuli were white uppercase L's, presented at four different orientations on a black background (0°, 90°, 180°, and 270°; see Figure 1). The target stimulus was a white uppercase T, presented either

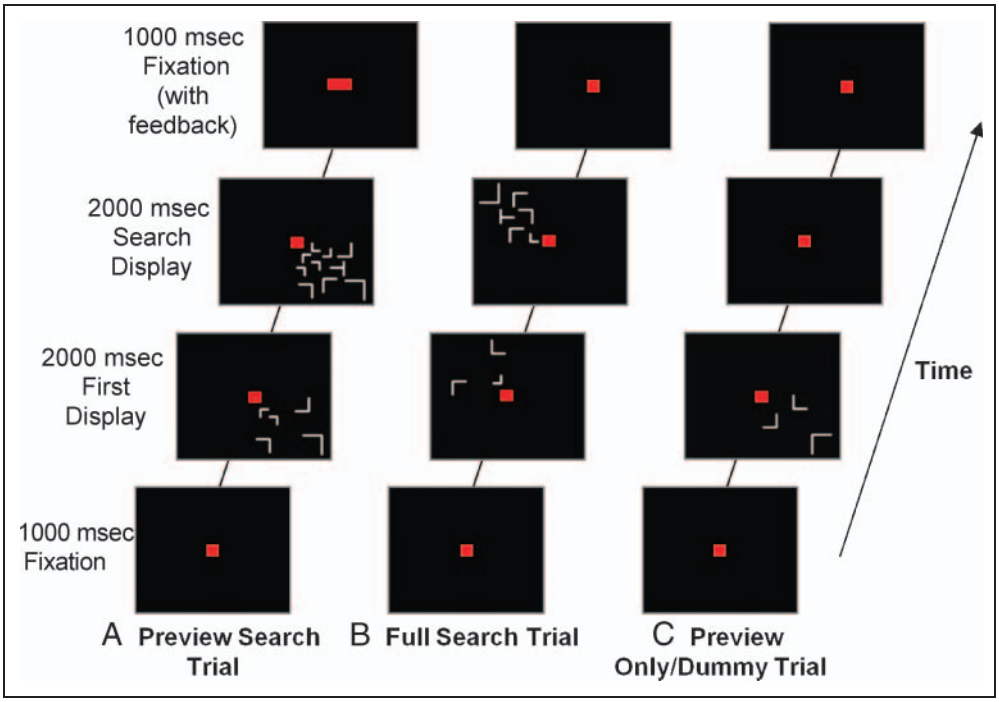

Figure 1. Experimental procedure and stimuli. Participants were instructed to fixate on the central square throughout the entire scan. (A) A preview search trial (10 items). The distracters in the first display remained on the screen when the remainder of the distracters and the target (a T tilted ±90° from vertical) appeared in the search display. (B) A full search trial (6 items). The first display was uninformative; the distracters offset at the start of the search display and were replaced with new distracters and a target in the same quadrant. The target always appeared in the search display for the preview search and full search trials. (C) A preview-only/dummy trial. No search display was presented for these trials. During the end fixation for the preview search and full search trials, the fixation square provided feedback; it changed to a rectangle if the response was incorrect (A).

90° right or 90° left of vertical (randomly on each trial). The two line components making up each letter were identical in length. The fixation consisted of a centrally located red square (0.27° × 0.27°, at a distance of 65 cm).

Possible stimulus locations were arranged on a circular 140-cell virtual matrix that consisted of eight concentric circular grids with radii of 1°, 2.1°, 3.2°, 4.9°, 7°, 9.1°, 11.2°, and 14°. Stimuli were scaled according to the human cortical magnification factor (Dougherty et al., 2003; Horton & Hoyt, 1991), resulting in 4, 8, 16, 12, 20, 24, 32, and 24 cells per circular grid. The stimuli presented on the three innermost circular grids subtended 0.63° × 0.63°, the next four grids presented stimuli subtending 1.37° × 1.37°, and the outermost ring presented stimuli subtending 2.41° × 2.41°. The display was divided along the vertical and horizontal meridians to create four quadrants resulting in 35 possible stimulus locations per quadrant. Stimuli were randomly assigned to cells in one quadrant for each trial, and were positioned in the center of each cell. There were two set sizes of 6 and 10 stimulus items.

Behavioral Methods

Participants completed four experimental scans (each 14 min 26 sec). Each scan consisted of two blocks of trials: a preview block and a full (baseline) block. There were two types of trial in the preview block: preview search (n = 20) and preview only (n = 12). A preview search trial was composed of two consecutive 2-sec displays. The first was the preview display which presented half of the distracter items (either 3 or 5) followed by the second, search, display, where the remainder of the distracter items (either 2 or 4) plus the target (always present) joined the previewed items on the screen. Participants indicated, using a response box held in the right hand, whether the T was tilted leftward or rightward. If a response was not made within 2 sec, it was counted as being incorrect. A preview-only trial consisted only of the initial preview display followed by 2 sec of fixation. Participants did not know when these trials would occur and were instructed not to respond on these trials. All trials began and finished with a 1-sec fixation, and feedback was given during the end fixation for a preview search trial via a change in shape of the fixation marker (see Figure 1A and C). Trial order and ITI length (between 4 and 12 sec) were randomly selected separately for each participant using Optseq2 (http://surfer.nmr.mgh.harvard.edu/optseq). For each combination of set size and quadrant there were 10 preview search trials and 6 preview-only trials across all four scans.

There were also two trial types in the full block: full search and dummy trials (see Figure 1B and C). These trials were identical to those in the preview block in terms of the trial numbers, trial sequence, set sizes, and presentation quadrants. However, for the full search trials, the 3 or 5 distracters presented in the first display disappeared with the onset of the search display and were replaced by 5 or 9 new distracters (plus the target) in the same quadrant. The final number of items in the search display of the

full search condition matched the final number in the preview search condition. The dummy trials were visually the same as preview-only trials.

The order of the two blocks within a scan was counterbalanced across participants and scans. Each scan began and ended with 30 sec of fixation. Prior to each block, there was a 3-sec instruction indicating the following block type. The two blocks were separated by a 31-sec fixation screen. Participants were instructed to fixate the central square for the entirety of the scan, and to use their peripheral vision to perform the task. Participants were encouraged to actively ignore the previewed distracters in the preview block and were informed that it would not be useful to ignore the distracters in the first displays of the trials in the full block. All participants undertook a practice session outside the scanner prior to the experiment (average correct performance = 84%).

fMRI Methods

Data were acquired using a 3-T Philips Achieva MRI scanner. Participants lay in the scanner and viewed the projector screen through a tilted mirror on the eight-channel SENSE head coil. If necessary, participants wore MRI-compatible glasses to correct vision. The BOLD signal was measured using a T2*-weighted echo-planar imaging sequence (with 32 ascending slices, a repetition time of 2000 msec, a time to echo of 35 msec, a flip angle of 85°, and a resolution of 2.5 mm^3). A T1-weighted high-resolution anatomical scan (1 mm^3) was acquired during the same session.

The fMRI Expert Analysis Tool (FEAT) Version 4.0.4 (part of FMRIB's software library, available at www.fmrib.ox.ac.uk/fsl) was used to process and analyze the data. Preprocessing of each functional scan involved head motion correction (absolute mean displacements per scan averaged across participants were 0.48, 0.56, 0.46, and 0.58 mm), slice-timing correction, nonbrain removal, spatial smoothing (5 mm full width at half maximum Gaussian kernel), intensity normalization and high-pass Gaussian-weighted temporal filtering (sigma = 50 sec). Each participant's functional dataset was registered with their anatomical image and then transformed into MNI space. Unexpected noise and artifacts were removed using Probabilistic Independent Component Analysis (Beckmann & Smith, 2004) implemented in MELODIC (Multivariate Exploratory Linear Decomposition into Independent Components), part of FMRIB's software library. Only 25 (of a total of 72) of the search scans required component removal, and of these scans, an average 3.8% of components were removed.

fMRI Analysis

General linear modeling analysis was conducted for each scan using FILM with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). A design matrix was created with 16 regressors representing each experimental condition according to the following factorial design: 4 (trial type: preview search, preview only, full search, and dummy) by 4 (quadrant: lower-left, lower-right, upper-left, and upper-right). Data were collapsed across set size. Preview search and full search trial regressors were defined as the duration from the onset of the first display to the response time. Preview-only and dummy trial regressors were the duration of the first display (i.e., 2 sec). Trials with incorrect responses were modeled as regressors of no interest as were the six movement parameters obtained during motion correction. All regressors were convolved with a gamma function.

Contrasts of interest included comparing preview-only trials with dummy trials for each quadrant separately. Similarly, contrasts were created to compare preview search with full search trials for each quadrant. Contrasts were combined across runs for each participant using fixed effects analysis. Group analysis was conducted using FMRIB's Local Analysis of Mixed Effects (Woolrich, Behrens, Bedell, Jenkinson, & Smith, 2004; Beckmann, Jenkinson, & Smith, 2003). Z (Gaussianized T/F) statistic images were thresholded using clusters with $Z > 2.1$ and a (corrected) cluster significance threshold of $p < .05$ (Worsley, Evans, Marrett, & Neelin, 1992) or an extent threshold of $k > 50$ and a significance threshold of $p = .05$. Group analyses included a prethreshold mask to limit results to the gray matter. Time-course data were extracted from each run for each participant using the Perl Event-related Average Time-course Extraction tool (www.jonaskaplan.com/peate).

Psychophysiological Interaction Analysis

We conducted psychophysiological interaction (PPI) analyses to examine brain activity functionally connected to activations identified with the main analyses. To create the source regions for the PPI analysis, the most significant voxel from each brain region was identified and a 6-mm spherical ROI was centered on this voxel. The mean activity time courses were extracted from the source regions of each of the participant's scans. The first level of an individual PPI analysis was conducted on each scan separately and included 16 regressors that represented the interaction between the time course of the source region and the 16 experimental conditions. Contrasts of interest were preview search–full search and preview only–dummy for each quadrant (and vice versa). Contrast images were entered into a fixed effects analysis to average data within each participant and a group-level mixed effects analysis $Z > 1.7$ and $p < .05$ was conducted (as above; Worsley et al., 1992).

RESULTS

Behavioral Data

Data were collapsed across the separate search scans and analyses were performed on the preview search trials and full search trials separately for each set size.

Table 1. Proportion of Correct Responses for Each Search Condition and Set Size

Set Size	*Full Search*	*Preview Search*
6	0.84	0.89
10	0.77	0.86

Accuracy

We recorded RTs and accuracy. All participants achieved 75% (or more) correct responses (Table 1). A repeated measures ANOVA with factors of condition (full search, preview search) and set size (6, 10 items) revealed significant main effects of condition [$F(1, 17) = 27.7$, $p = .00006$, partial $\eta^2 = 0.62$] and set size [$F(1, 17) = 15.8$, $p = .001$, partial $\eta^2 = 0.48$], and no significant interaction [$F(1, 17) = 1.6$, $p = .22$, partial $\eta^2 = 0.87$]. Because there was a response deadline in the experiment (2 sec, after which responses were recorded as errors), the significant effects of condition and set size were not unexpected. RTs were longer in both the full condition and at the larger set size, thus there was a speed–accuracy tradeoff.

Reaction Times

We used an adjusted response time measure (RTadj) instead of RT as the dependent measure due to the restricted response period. We divided the average correct RT for each participant, condition, and set size combination by the proportion correct for that combination. We used this adjustment in a recent study (Allen et al., 2008) where the error rates were also inflated by a response deadline. Figure 2A plots the RTadj against set size for the full search and preview search conditions.

RTadj data for the correct trials were entered into a repeated measures ANOVA with main factors of condition (preview search, full search) and set size (6, 10 items). Despite there being no significant interaction between condition and set size [$F(1, 17) = 1.9$, $p = .19$, partial $\eta^2 = 0.1$], performance on full search was significantly slower than that in preview search [$F(1, 17) = 54$, $p = .000001$, partial $\eta^2 = 0.76$], suggesting an advantage of the preview display. Participants were slower with more display items [$F(1, 17) = 33.6$, $p = .00002$, partial $\eta^2 = 0.66$].

Inspection of individual participant data revealed variations in preview benefit across participants, enabling us to categorize participants as "previewers" and "non-previewers." A total of 12 of the 18 participants were classified as previewers, identified strictly as those displaying the standard preview benefit (Watson & Humphreys, 1997) measured in terms of an improvement of search efficiency (in terms of time per item) in the preview condition compared to the full condition. An ANOVA revealed a significant interaction between condition and set size for these participants [$F(1, 11) = 15.4$, $p = .002$, partial $\eta^2 = 0.58$; Figure 2B]. There was also a significant interaction between condition and set size for the non-previewers [$F(1, 5) = 14.2$, $p = .013$, partial $\eta^2 = 0.74$], although the full and preview search slope functions did not conform to the standard preview benefit (Figure 2C).

In a similar vein, we observed that there was considerable variation in preview benefit across quadrants (Figure 3A–D). For each participant, we calculated RTadj for each quadrant, set size, and search condition combination, and separate ANOVAs for each quadrant (including all participants) revealed a significant interaction between condition and display size for only the lower-left quadrant [$F(1, 17) = 12$, $p = .003$, partial $\eta^2 = 0.41$]. Thus, the best preview benefit was found in the lower-left quadrant where search efficiency for the preview search condition was significantly better than the efficiency in the full search condition. Furthermore, 13 of the 18 participants displayed a clear preview benefit in terms of slope differences between the conditions in the lower-left quadrant. Nine participants previewed in the lower-right and upper-right quadrants, whereas only six participants previewed in the upper-left

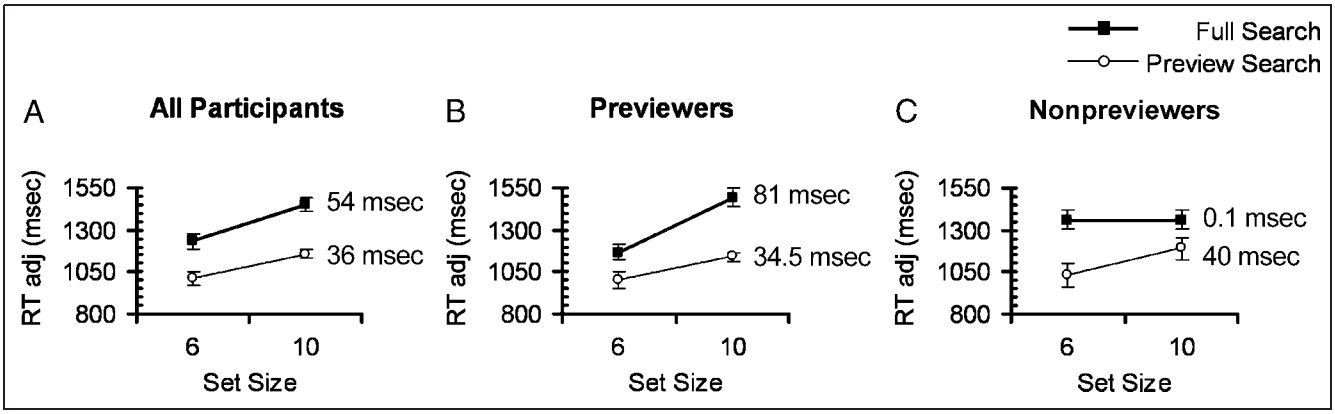

Figure 2. Adjusted reaction times (RTadj) plotted against set size for the full (filled squares) and preview (unfilled circles) search conditions averaged across (A) all participants ($n = 18$), (B) previewers ($n = 12$), and (C) non-previewers ($n = 6$). RTadj is measured by RT/proportion correct. The slope function in terms of time (msec) per search item for each condition is reported. Vertical bars represent ±1 standard error.

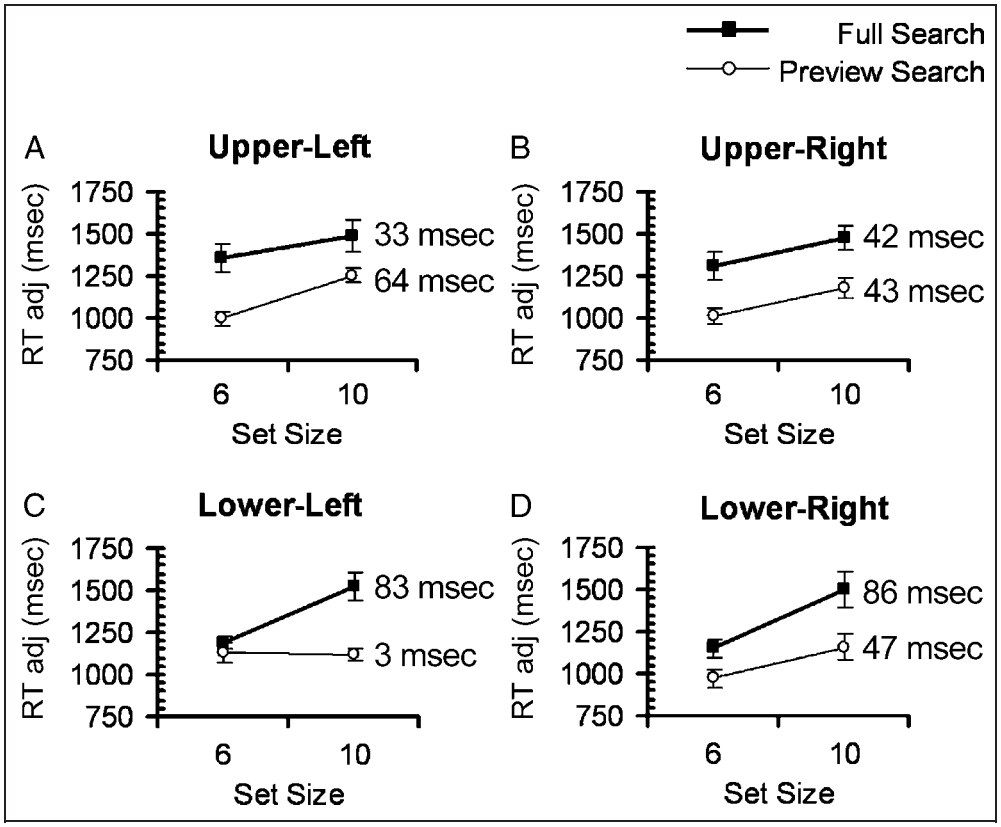

Figure 3. Adjusted reaction times (RTadj) plotted against set size for the full (filled squares) and preview (unfilled circles) search conditions averaged across all participants (n = 18). The search slopes are plotted for each quadrant separately: (A) upper-left quadrant, (B) upper-right quadrant, (C) lower-left quadrant, and (D) lower-right quadrant. The slope function in terms of time (msec) per search item for each condition is reported. Vertical bars represent ±1 standard error.

quadrant. Note that the search slopes in the lower-right quadrant (Figure 3D) indicate a standard preview benefit for this quadrant, although this is not significant (p = .26).

It is unclear why there are stronger preview benefits in the lower visual field (although it is consistent with attention studies that report a lower visual field advantage for tasks involving attention, e.g., He, Cavanagh, & Intriligator, 1996). It is possible that the unusual viewing conditions made it easier (or more difficult) to direct attention to (or from) certain locations. We used the differences in preview benefit between quadrants, as well as between previewing and nonpreviewing participants, to search for BOLD activity specifically linked to successful preview by incorporating these behavioral variations into the fMRI analyses. Because the behavioral preview benefit was stronger in some quadrants and participants, this allows us to find the neural signature relating to a successful preview benefit while removing activity relating to merely searching the stimuli or intent to preview.

Imaging Data

fMRI data from all scans from one participant and from two scans belonging to another participant were discarded due to excessive head movement.

Preview-related Neural Activity

First, we identified brain areas showing preview-related activity. Preview search/only trials were contrasted against full search/dummy trials. Preview activity in behavioral non-previewers was deducted from preview activity in behavioral previewers (Table 2). Supporting previous findings (Dent et al., in press; Allen et al., 2008; Olivers et al., 2005; Pollmann et al., 2003), we find activation in the precuneus and SPL that corresponds with ignoring the preview display. Regardless of what attentional task a participant intends to perform, they will only be successful if the correct neural messages are passed to earlier cortical stages. If the intent is to attend to a particular target, but the appropriate stimulus-specific neurons are not modulated, then the target will not be enhanced, for example. Here, only some of our participants and quadrants generated a preview benefit (see above). Thus, we can assume that the activation patterns that underlie the preview benefit will be stronger in the more successful preview trials. In our data, regions such as the SPL were more activated when previewers (as opposed to non-previewers) had greater preview benefit, which suggested that this was the case (Supplementary Figure).

Linking Preview-related Neural Activity with Behavioral Preview Benefit

Here, the critical comparison is between preview-only and dummy trials as this reveals processes involved with active ignoring without contamination from the search displays. For each participant and quadrant separately, dummy trials were deducted from preview-only trials. Because we were interested in trials where the intent to preview was

Table 2. Areas of Significant Clusters of Preview-related Activity, Averaged across Quadrants, for Behavioral Previewers Compared to Non-previewers (Extent Threshold = 50, $p = .05$)

Contrast	*Structure*	*Location x, y, z (mm)*	*Z Score*	*Volume (Voxels)*
Preview (search and only)–full (search and dummy)	L Lateral occipital cortex/precuneus	−24, −64, 32	2.56	239
	L Lateral occipital cortex	−42, −74, 16	2.84	115
	L Precuneus	−12, −54, 56	2.14	75
	L Precentral gyrus	−24, −6, 46	3	67
	L Supramarginal gyrus	−54, −24, 26	2.33	67
	L Superior frontal gyrus	0, 32, 52	2.22	59
Preview only–dummy	L Lateral occipital cortex/precuneus	−22, −64, 32	3.07	414
	R Precentral gyrus	48, 4, 26	2.25	194
	R Lateral occipital cortex/SPL	36, −62, 52	2.73	80
	L Lateral occipital cortex	−42, −74, 16	2.41	71
	L Cingulate gyrus	−6, −28, 34	2.44	50
	R Cingulate gyrus	10, −42, 38	2.14	50
Preview search–full search	L Lateral occipital cortex/SPL	−28, −62, 60	2.64	189
	L Postcentral gyrus	−52, −26, 50	2.38	100
	L Lateral occipital cortex	−40, −74, 16	2.54	92
	L Precentral gyrus	−24, −6, 48	3.44	91
	R Middle temporal gyrus	46, −46, 12	2.7	69

successfully carried out, quadrants that participants previewed in were compared to those quadrants in which participants did not preview. There were three clusters where activity was greater for previewers compared to non-previewers (Table 3, Figure 4).

Supporting previous findings (Dent et al., in press; Allen et al., 2008; Olivers et al., 2005; Pollmann et al., 2003), we found activation in the left and right precuneus corresponding to ignoring the preview display. Secondly, the results indicate that actively ignoring visual information leads to signal changes in early visual cortex.

To investigate whether actively preparing to ignore increased activation in the precuneus and visual cortex, we extracted the mean BOLD activity from these areas for the preview only–dummy contrast for each quadrant and participant and correlated these signals with the magnitude of behavioral preview benefit (Figure 5A–D). We extracted the mean BOLD signal (using Featquery) from spherical ROIs of 6 mm radius centered on the maximally activated peak voxels in the left precuneus (−8, −78, 40), right precuneus (14, −82, 42), left intracalcarine cortex (−10, −90, −2), and left occipital fusiform gyrus (−16, −88, −10). To calculate the magnitude of behavioral preview benefit for each participant and quadrant, we used Equation 1:

$$\text{Preview Benefit} = \frac{\text{Efficiency : Full Search} + c}{\text{Efficiency : Preview Search} + c} \quad (1)$$

where c is a constant added to reflect that slopes occasionally decreased with increasing set size in the preview condition. The behavioral preview benefit was significantly correlated with activation in left intracalcarine cortex and the left precuneus but not with the right precuneus and left occipital fusiform gyrus.

We further examined the fMRI data in response to preview-only and dummy trials presented to the quadrant (lower-left) that showed the strongest benefit from preview. This contrast revealed significantly greater preview activity for the behavioral previewers compared to the non-previewers in occipital cortex (Table 4). Importantly, the focus of activation in visual cortex is located above the calcarine sulcus in the right hemisphere, that is, contralateral to the visual field of stimulation, and thus, corresponds to the known retinotopic anatomy of early visual cortex.

As predicted by the behavioral data, there was no significant preview-related neural activity from the other presentation quadrants. However, with a threshold of $p = .01$ (uncorrected, $k > 50$), an area of early visual cortical activity (−18, −104, 0; 110 voxels) related to successful previewing was identified in the left hemisphere for the lower-right quadrant (i.e., contralateral to the visual field of stimulation). There were no ($k > 50$) areas of activation in visual regions for the upper-left and upper-right quadrant analyses using the uncorrected threshold.

Table 3. Three Clusters of Significant Activations for the Preview-only–Dummy Contrast for Quadrants in Which Participants Behaviorally Previewed Compared to Quadrants in Which Participants Did Not Preview (Cluster Threshold $Z = 2.1$, $p < .05$)

Structure	*Location x, y, z (mm)*	*Z Score*	*Volume (Voxels)*
Left Occipital			
L Occipital fusiform gyrus extending to:	−16, −88, −10	3.45	1556
–L Intracalcarine cortex	−10, −90, −2; 0, −94, 4		
–L Lateral occipital cortex	−44, −72, −10; −36, −86, 2		
–L Lingual gyrus	−6, −76, −8		
Left Medial			
L Occipital cortex extending to:	−30, −92, 24	3.76	645
–L Precuneus	−8, −78, 40; −10, −76, 54; −6, −70, 56; −6, −80, 52		
–L Lateral occipital cortex	−16, −86, 42		
Right Medial			
R Lateral occipital cortex extending to:	44, −58, 54	3.64	1199
–R Angular gyrus	42, −54, 56; 50, −52, 56		
–R Precuneus	14, −82, 42		
–R Lateral occipital cortex	50, −58, 52; 26, −70, 46		

Psychophysiological Interaction

We performed functional connectivity analyses to identify the contribution of the precuneus to activity in other brain regions. We examined whether the coupling between the precuneus and other brain areas differed depending on whether the observers were actively ignoring items in the first display (i.e., preview condition) compared to when

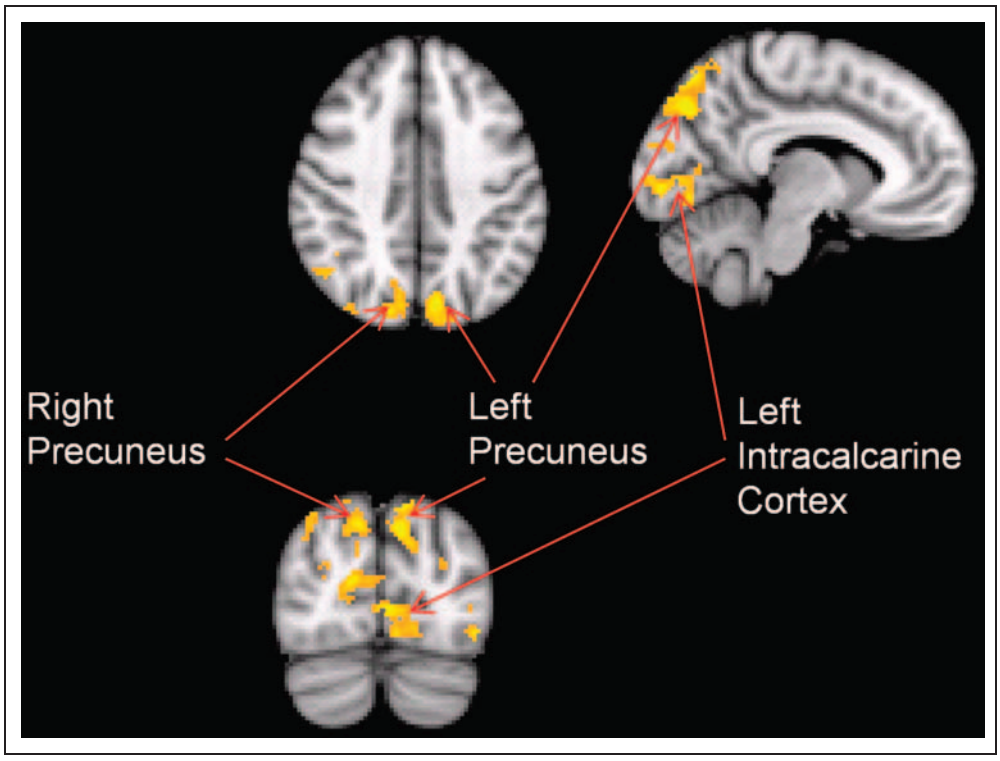

Figure 4. Preview-related group activation revealed from the preview only–dummy contrast for quadrants in which participants behaviorally previewed compared to those quadrants in which participants did not preview (presented on the MNI template brain).

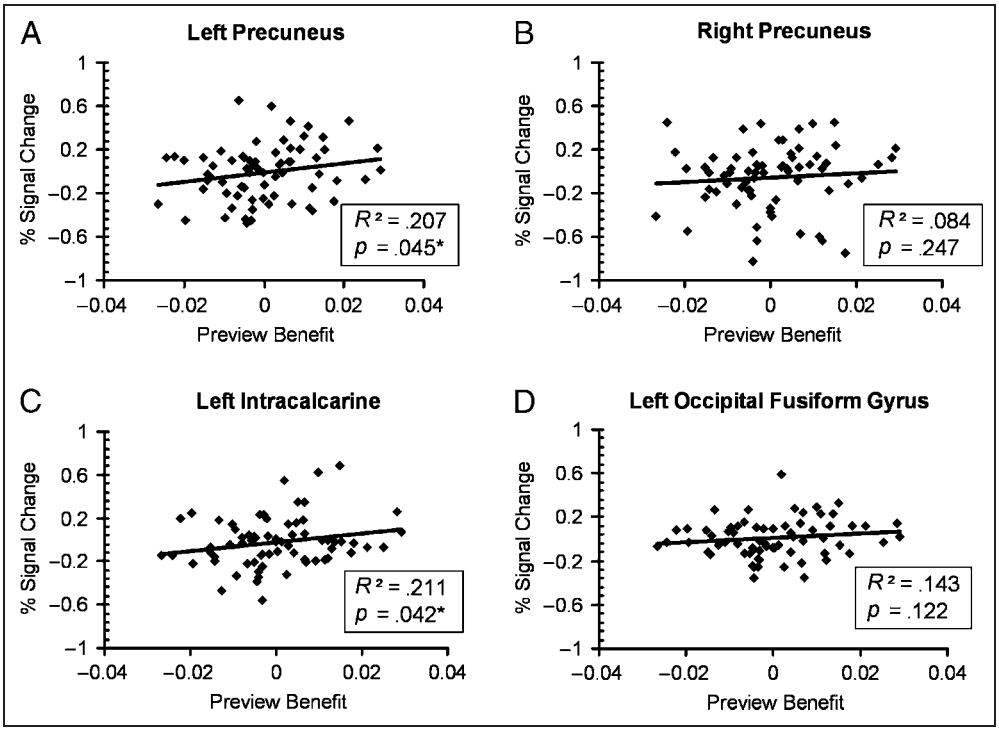

Figure 5. The magnitude of behavioral preview benefit plotted against mean BOLD signal extracted from the (A) left precuneus, (B) right precuneus, (C) left intracalcarine cortex, and (D) left occipital fusiform gyrus for the preview only–dummy contrast for each participant and quadrant. One-tailed Pearson's R^2 and p values are indicated for each area. Each point represents data from each quadrant for each participant ($n = 68$). *$p < .05$.

they were not (i.e., full condition). We seeded the separate PPI analyses in the left (centered at −8, −78, 40) and right precuneus (centered at 14, −82, 42). The PPI analysis using the right precuneus as the source region revealed that there was differential activation within regions of the fronto-parietal attention network depending on whether participants were undertaking the dummy condition or the preview-only condition and whether participants were previewers or non-previewers. We found that for those participants who benefited from the preview, the right precuneus interacted significantly with the postcentral and the precentral gyri when participants were completing the dummy condition in comparison to the preview-only condition (see Table 5 and Figure 6). Similar clusters of activation (R precentral gyrus = 14, −30, 70; L postcentral gyrus = −56, −18, 34) were found for the left precuneus source region with a threshold of $p = .01$ (uncorrected, $k > 50$). Precuneus activity during preview-only trials, relative to dummy trials, was thus related to a decrease in preview-related activation in attentional control areas (Corbetta & Shulman, 2002).

For the PPI analyses contrasting full search with preview search, for those participants who benefited from the preview, both the left and right precuneus interacted significantly with visual cortical regions when participants were completing the full search condition in comparison to the preview search condition (Table 5, Figure 6). Precuneus activity during preview search trials was thus related to a decrease in search-related activation in visual cortex (relative to full search trials). Of particular interest here is that there is significant activation in *early* visual cortex, specifically in intracalcarine cortex (−16, −70, 4). Other areas of activation that overlap across the two analyses include left lateral occipital cortex and right cuneal cortex.

DISCUSSION

Extending previous studies, we found that (Dent et al., in press; Allen et al., 2008; Olivers et al., 2005; Pollmann et al., 2003) precuneus activation was associated with successfully ignoring distractors. Second, preparatory-related

Table 4. Areas of Significant Activations for the Preview Only–Dummy Contrast in the Lower-left Quadrant for Behavioral Previewers Compared to Non-previewers (Cluster Threshold $Z = 2.1$, $p < .05$)

Structure	*Location x, y, z (mm)*	*Z Score*	*Volume (Voxels)*
R Intracalcarine cortex extending to:	6, −82, 10	3.33	901
–R Occipital pole	8, −92, 20		
–R Lingual gyrus	8, −74, −4; 4, −82, −8		
–L Lingual gyrus	−4, −74, −6		

Table 5. Areas That Significantly Interact with the L Precuneus and the R Precuneus for the Dummy/Full Search–Preview-only/Preview Search Contrasts for Quadrants in Which Participants Behaviorally Previewed Compared to Quadrants in Which Participants Did Not Preview (Cluster Threshold $Z = 1.7$, $p < .05$)

Contrast	*Structure*	*Location x, y, z (mm)*	*Z Score*	*Volume (Voxels)*
Dummy–preview only	Source region: R Precuneus			
	L Postcentral gyrus extending to:	−32, −36, 70	3.45	1466
	–R Precentral gyrus	24, −22, 62; 10, −30, 74; 22, −26, 74		
	–R Postcentral gyrus	16, −30, 70		
Full search–preview search	Source region: L Precuneus			
	L Cuneal cortex extending to:	−8, −88, 24	3.58	4712
	–L Intracalcarine cortex	−16, −70, 4		
	–L Lateral occipital cortex	−22, −82, 36; −28, −72, 20		
	–R Cuneal cortex	8, −84, 40; 18, −72, 24		
	Source region: R Precuneus			
	L Lateral occipital cortex extending to:	−24, −82, 38	4.13	5628
	–L Intracalcarine cortex	−16, −78, 2; −16, −70, 4		
	–R Cuneal cortex	18, −70, 22		
	–R Lateral occipital cortex	16, −84, 38		

activity also increased neural activity in early visual cortex during this active ignoring process. Third, precentral and postcentral gyri activation (part of the fronto-parietal attention network), driven by the precuneus, was reduced when successful previewers were preparing to ignore distracters. Fourth, search-related activation in early visual cortex, driven by the precuneus, was reduced when participants were able to successfully ignore early presented distracters.

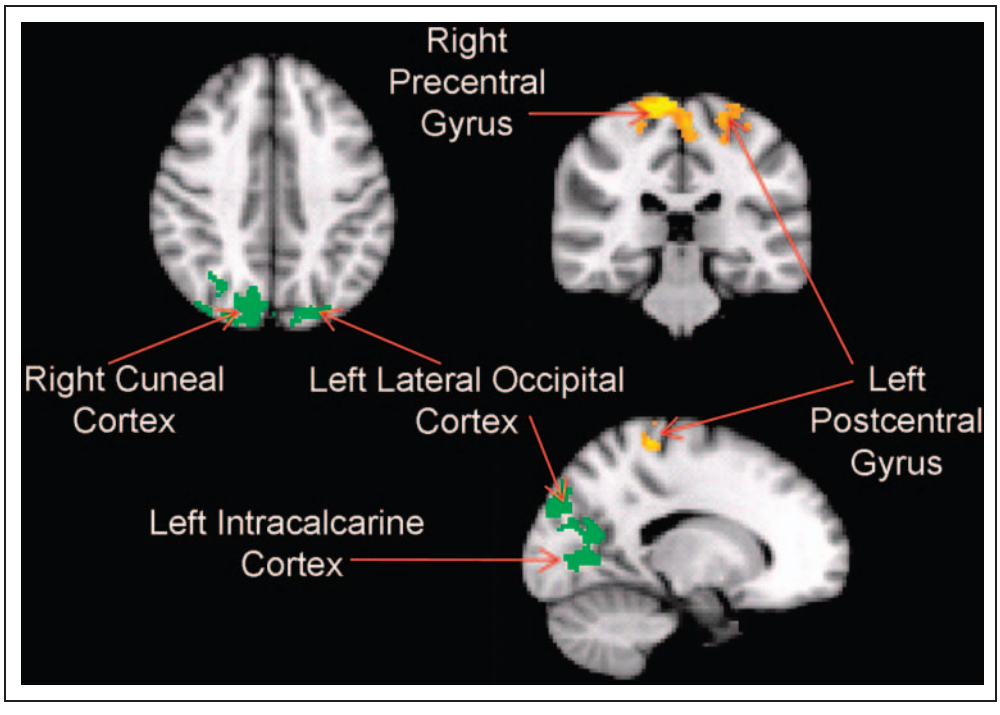

Figure 6. Results of PPI analyses. Yellow: BOLD activity driven by the right precuneus when previewing participants (relative to non-previewers) completed the dummy trials relative to the preview-only trials. Green: BOLD activity driven by both the left precuneus and the right precuneus when previewing participants (relative to non-previewers) completed the full search trials relative to the preview search trials. Activations are presented on the MNI template brain.

Preview-related Preparatory Activity in Early Visual Cortex

Previous studies have demonstrated preparatory activity in visual cortex for targets (Macaluso et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999) and distracters (Ruff & Driver, 2006; Serences et al., 2004). Here, preparatory activity associated with previewing irrelevant distracters occurred in early visual cortex and could be easily separated from target-related activity. Our results demonstrate increased neural activity in primary visual cortex (in likely V1 identified using WFU PickAtlas: Maldjian, Laurienti, Kraft, & Burdette, 2003) that was quadrant specific. Consistent with the finding that increased preview-related BOLD activation in early visual cortex is correlated with the magnitude of behavioral preview benefit, the trials presented to the upper visual quadrants did not display a behavioral preview benefit or enhanced neural activity. The asymmetry of preview performance between upper and lower visual quadrants may be explained by a commonly reported behavioral finding that visual processing is enhanced in the lower visual field compared to the upper visual field (e.g., Danckert & Goodale, 2001; Rubin, Nakayama, & Shapley, 1996). In particular, it has been reported that there is an advantage for attentional processing in the lower visual field (He et al., 1996). The portion of visual cortex in the macaque monkey brain that represents the lower visual field projects considerably more to posterior parietal cortex, an area involved with spatial attention, than does the portion that represents the upper visual field (Maunsell & Newsome, 1987). This may explain the lower visual field advantage with attentional tasks in humans. However, the asymmetry seen here is weak with only the lower-left quadrant showing a significant advantage for the preview condition. Further research is required to assess the specificity of the preview benefit to visual field location.

Precuneus Activity

There was a bilateral increase in precuneus neural activity for the preview-only trials relative to the dummy trials. The precuneus is consistently activated (Dent et al., in press; Allen et al., 2008; Olivers et al., 2005; Pollmann et al., 2003) in response to preview trials, suggesting this region plays a critical role in visual marking. This brain area is thought to be involved with a variety of higher-level cognitive functions including episodic memory, consciousness, and visual–spatial imagery (see Cavanna & Trimble, 2006 for a review). Allen et al. (2008) found that the precuneus was activated both by a visual working memory task and by a preview search task, and that the former could interfere with the latter. This provides evidence that the precuneus is involved with encoding the spatial representations of the old, to-be-inhibited, items in memory. Indeed, a secondary auditory task did not interfere with the preview task if it was presented 1 sec after the presentation of the preview, whereas a secondary visual task did interfere, implying that the visual memory representation of the old distracter items is critical (Humphreys et al., 2002).

Functional Connectivity Analysis

We report that activity in the precuneus is more connected with fronto-parietal activation for the dummy condition relative to the preview-only condition in successful previewers. The pre/postcentral cortical activation we discerned has been implicated in several functional imaging studies that have used spatial attention tasks (Donner et al., 2000; Culham et al., 1998; see Corbetta & Shulman, 2002 for a review). Although often considered to be passively viewed, the dummy trials informed observers as to the location of the subsequent stimulus and to prepare for a relatively difficult search task. It seems reasonable, therefore, that there is a strong connection with areas involved in attentional control and orienting in these trials. In support, a visual search study by Weidner, Krummenacher, Reimann, Müller, and Fink (2008) found that decreased target saliency increased BOLD activation in several areas of the fronto-parietal attention network, including pre/postcentral cortex. For preview search, it seems that these orienting signals are comparatively weak in comparison to the preview-related activity.

We also report that activity in the precuneus is related to decreases in early visual cortex activation for the preview search condition relative to the full search condition in successful previewers. This is in contrast to the increase in early visual activation for the preview-only condition relative to the dummy. Thus, it seems that in early visual cortex, successful ignoring of the previewed distracters is related to, first, an increase in activity but also an overall down modulation of activity by the precuneus. This is consistent with recent studies comparing distracter encoding during the preview display that also show an increase in activity associated with the preview benefit (Allen et al., 2008; Pollmann et al., 2003). Similarly, Humphreys et al. (2004) presented probe dots early (200 msec) and late (800 msec) in a preview display. As with previous probe-dot detection studies (Olivers & Humphreys, 2002; Watson & Humphreys, 2000), late probes gave rise to longer RTs when they appeared at the locations of the old distracters than when they occurred at the location of the new distracters, suggesting inhibition of the old distracters. However, detection of early probes was actually *facilitated*, suggesting that participants initially attend to the old distracters before inhibiting them. Similarly, results from an event-related potential study (Belopolsky, Peterson, & Kramer, 2005) suggest that the inhibition of old distracters is applied toward the end of the preview interval. Of course, such an explanation requires that a decrease in BOLD signal means a decrease in neural activity (see Shmuel, Augath, Oeltermann, & Logothetis, 2006).

The processes underlying the preview benefit can be separated into two components (Humphreys et al., 2002).

First, observers attend and encode the previewed distracters to form a representation of the items in memory. Second, this representation is inhibited and the new items are prioritized. Thus, the increased activation for preview during the first display is likely to represent active attentional encoding of the distracters. The decreased activation for preview (relative to full search) is likely to reflect that in the full search condition there were effectively more items to search through. It is important to note, however, that the data cannot tell us whether activation in the preview search condition was suppressed relative to the full search condition or whether activation in the full search condition was increased relative to the preview search condition.

Conclusion

We used the preview search paradigm to investigate whether there are neural signatures relating to ignoring known distracters. We found that in order to benefit from the preview, observers must prepare to inhibit old distracters, leading to an increase in activation in visual and parietal regions. Subsequently, further processing of these items is suppressed. The precuneus is likely to be involved with representation of the previewed distracters and our results suggest that the precuneus modulates activity in early visual cortex. In particular, the precuneus is involved with inhibiting further processing in visual cortex of the encoded, but excluded, distracters.

Reprint requests should be sent to Harriet A. Allen, Brain and Behavioural Sciences, School of Psychology, University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom, or via e-mail: h.a.allen@bham.ac.uk.

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